



Original Article

Trait-based metrics as bioindicators: Responses of stream fish assemblages to a gradient of environmental degradation



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ABSTRACT

The development of biomonitoring tools is increasingly appealing in light of the increasing degradation of aquatic ecosystems. In this context, we investigated the responses of stream fish communities to the gradient of environmental degradation in different basins using a variety of indices based on functional diversity, functional composition, and taxonomic diversity. We used datasets from three Brazilian ecoregions. In order to describe the gradient of environmental degradation we scored streams based on local and landscape variables. The functional structure of the assemblages was described in relation to seven functional traits related to habitat use, swimming capacity, and maneuverability. We described assemblages in each ecoregion separately in relation to 20 potential indicators, grouped in four families: indices of functional diversity based on presence/absence ($FD_{p/a}$); indices of functional diversity weighted by abundance (FD_{abund}); indices of functional composition (mT); and, indices based on taxonomic diversity (TDiv). The relationship between the indicators and the gradient of environmental degradation were evaluated using linear regression. We found a significant interaction effect (ANOVA, $p = 0.006$) between group of indices and ecoregions for the performance of indicators, suggesting a context-dependent response. The indices, on an individual basis, had variable performance and consistency among ecoregions. Four mT indicators demonstrated the highest average performance and consistency. Taxonomic diversity indicators consistently had the lowest average performance, while $FD_{p/a}$ and FD_{abund} indicators had low average performance and variable inter-regional consistency. The differential inter-regional performance of indicators was due to the differences in the lengths of the gradients of environmental degradation. Our results indicate that functional traits have greater predictive power compared to taxonomic indicators for fish responses to a gradient of environmental degradation. Although indicators of functional composition are the most promising, we emphasize that caution is needed when generalizing functional diversity indicators across ecoregions because most of them are context-dependent.

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1. Introduction

The search for biological correlates for environmental gradients is a fundamental step for using biological indicators in ecosystem quality assessments. However, bioindicators tend to present high variability in responses across different ecoregions, and therefore their use is usually context-dependent (Bonada et al., 2006). One of the main reasons for the non-transferability or limited usefulness of biological metrics across ecoregions is the difference in species

composition; this is notably the case for metrics based on the taxonomic identity of species (Tolkamp, 1985). In view of this limitation, functional traits arose as good candidates and ecologically meaningful metrics for biomonitoring (functional trait indicators, *sensu* Moretti et al., 2009), and presumably are broadly applicable over biogeographic boundaries (Statzner et al., 2001). However, more extensive validation remains to be done, since the capacity of these indices in discriminating environmental gradients (i.e., performance) among taxa and ecosystems varies considerably (Moretti et al., 2009; Vandewalle et al., 2010).

The habitat templet (Southwood, 1977) and the habitat-filtering concepts (Tonn et al., 1990) provide a sound theoretical framework supporting the idea that communities described based on

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species traits should reveal convergent patterns. These theories have been extended for lotic ecosystems (Poff, 1997; Townsend and Hildrew, 1994) and show strong predictive power (Ibañez et al., 2009), with enormous potential for applied purposes. Indeed, there is an increasing trend of including trait-based approaches in monitoring and river assessments (Dolédec et al., 1999; Pont et al., 2006). More importantly, the trait-based approach provides a more mechanistic perspective of the species–environment relationship, since the response of a species to environmental gradients is determined by the set of traits influencing its performance and persistence (Violle et al., 2007).

Functional trait indicators can be summarized in two groups. One is based on the mean trait values (mT – mean of traits, *sensu* Moretti et al., 2009), representing the dominant functional attribute in a community (Lavorel et al., 2008). The other is based on the range of traits in the community (i.e., FD – functional diversity, *sensu* Moretti et al., 2009), that, in turn, may be expressed by different metrics (e.g., Laliberté and Legendre, 2010; Petchey and Gaston, 2002; Villéger et al., 2008). Some indices include species abundance in their calculation and others do not. This feature may have consequences for how well the metrics will predict environmental gradients (de Bello et al., 2007; Mouillot et al., 2013a). For example, FD indices based on presence/absence (FD_{p/a}) are influenced by loss or gain of functional traits in the community, which means that their change depends on extirpation or addition of species with particular traits in the community. By contrast, FD metrics based on species abundance (FD_{abund}) may detect changes in assemblages associated with changes in species abundance, before the loss of species occurs, making them potentially more sensitive to environmental changes (Mouillot et al., 2013a). Therefore, we may expect that FD_{p/a} and FD_{abund} would perform differently depending on how broad the environmental gradient is, with FD_{p/a} better predicting changes in assemblages along a broader environmental gradient, due to the high turnover of species and traits. Conversely, FD_{abund} would be a better indicator for narrower gradients, where changes in relative abundance among species are expected to be more important than species turnover. Finally, changes in abundance and species turnover while maintaining overall diversity could influence mT because dominant traits would respond to filters operating across the gradient (Keck et al., 2014).

Stream fish assemblages respond markedly to human impacts in the aquatic environment (e.g., habitat degradation), but also to the alteration in landscape context (e.g., land use conversion) (Allan, 2004). The response of stream fish to land use and habitat degradation has been widely assessed from a taxonomic perspective (Allan, 2004; Casatti et al., 2006; Esselman and Allan, 2010), but more recently, the influences on the functional structure of assemblages have also been studied. The functional composition and functional diversity of stream fish communities have been shown to vary predictably along environmental gradients and human impacts (Pool et al., 2010; Casatti et al., 2012; Keck et al., 2014). Loss of benthic and rheophilic species, poorly adapted for physical habitat degradation, while allowing colonization by pool-dwelling species are examples of trait-mediate changes in assemblage structure along gradients of physical habitat degradation (Casatti et al., 2012). Therefore, fish represent a potential target group for ecosystem quality assessment through a multifaceted approach.

In this context, the aim of our study was to investigate the capability of different diversity indicators to summarize the responses of fish communities across environmental gradients in streams. More specifically, we evaluated which indicators (taxonomic diversity, mT, FD_{p/a}, and FD_{abund}) performed best at discriminating stream assemblages across gradients of land use and habitat degradation. We studied the response of fish assemblages in three distinct Neotropical ecoregions, Tocantins-Araguaia (TA); Upper Paraná (UPA), and Madeira Brazilian Shield (MA), which have different

intensities and histories of land use. These differences allowed us to test to what extent the response of stream fish assemblages to anthropogenic environmental gradients can be generalized. Near pristine streams predominate in TA, as the landscape is still little impacted by anthropogenic activities (Borges et al., 2015), contrasting with UPA in the southeast of Brazil, where streams drain landscapes with higher levels of anthropogenic impacts, as this region lacks large forest remnants (Casatti et al., 2015a). The gradient of environmental degradation is broader in MA, with stream drainages varying from highly degraded to entirely forested (Bordignon et al., 2015).

We expect that functional indicators of diversity would outperform taxonomic indicators in predicting the gradient of environmental degradation, but that metrics would differ in their performance according to the differences in the gradient length. Indicators of functional diversity (FD_{p/a} and FD_{abund}) and functional composition (mT) should be able to better explain variation in the structure of assemblages in ecoregions with broader gradients (i.e., the Madeira ecoregion), because environmental changes should be enough to alter relative abundance and species composition. Furthermore, the predictive power of functional diversity metrics weighted by abundance (FD_{abund}) and functional composition (mT) should be greater in regions with narrower gradients (i.e., the Tocantins-Araguaia and Upper Paraná ecoregions) because, in these conditions, changes in species abundance are more important than changes in species composition. Therefore, we predict that the correlation between fish indicators with the gradient of environmental degradation will vary among group of indicators and among ecoregions, with different indicators performing better in specific contexts.

2. Material and methods

2.1. General sampling design and study area

In order to assess the performance of each indicator at predicting the gradient of environmental degradation, we correlated ten FD, seven mT, and three taxonomic indices for stream fish communities at the reach scale with an environmental gradient summarizing the land use and habitat conditions. We used three sets of data gathered from three different ecoregions of Brazil (*sensu* Abell et al., 2008): the Machado River basin, Madeira Brazilian Shield ecoregion (MA); the Santa Teresa basin, Tocantins-Araguaia ecoregion (TA); and the São José dos Dourados/Turvo-Grande basin, Upper Paraná ecoregion (UPA) (Fig. 1). The spatial extents within each region were about 460 km in MA, 100 km in TA, and 300 km in UPA (Fig. 1).

The Machado River basin drains the most populated area of the State of Rondônia, in Northern Brazil, with a total catchment area of 75,400 km². This region has been altered by anthropogenic activities since 1970, with settlements along the highway BR-364 (Alves et al., 1998). The watersheds that form the Machado River basin are covered by forests (mature and secondary, ranging from 0 to 100% coverage) or grasslands which are used as pasture for cattle ranching (Fernandes and Guimarães, 2002).

The Santa Teresa River basin belongs to the Upper Tocantins River system, a macro-regional division of the Tocantins-Araguaia ecoregion. This basin is in the Cerrado biome (Brazilian savanna). Human occupation started around 1930 and has been intensifying since 1970, with the building of the Belém-Brasília highway, which has stimulated the conversion of native coverage to pasture for livestock grazing (Ministério do Meio Ambiente, 2006). Despite land conversion, the Santa Teresa basin still harbors approximately 70% of the native vegetation, mainly in the highest portions of the basin (Borges et al., 2015).

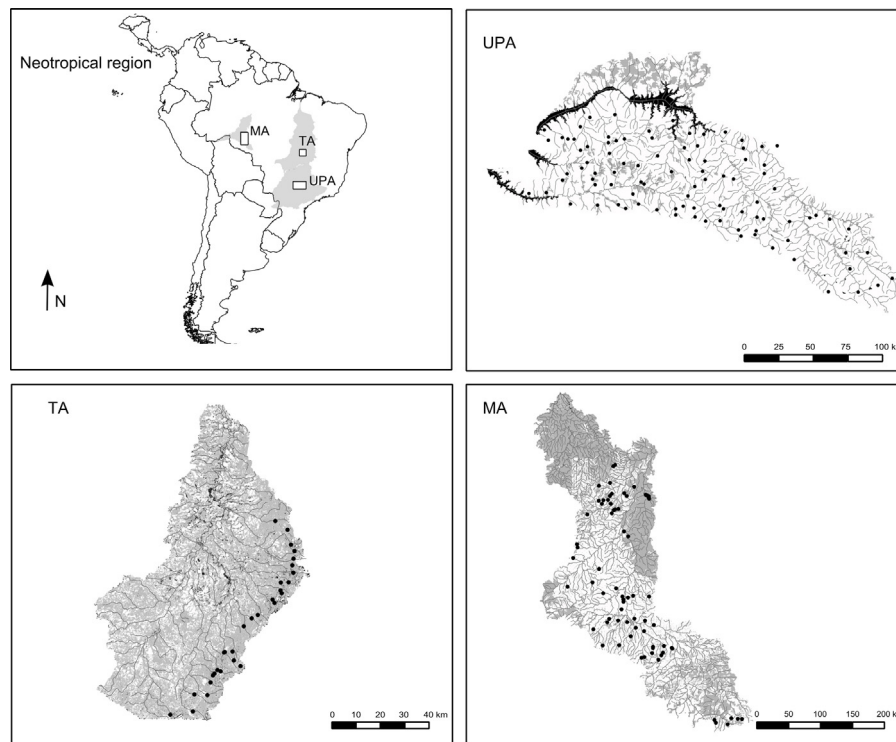


Fig. 1. Sampled streams in the three ecoregions, Tocantins-Araguaia (TA), Madeira Brazilian Shield (MA), and Upper Paraná (UPA). Gray areas on the map of each ecoregion are native vegetation remnants.

The São José dos Dourados and Turvo-Grande rivers drain the northwest region of the State of São Paulo, located in southeastern Brazil. This region was originally covered by Semi-Deciduous Seasonal forests (Silva et al., 2007). Since the second half of the 20th century, this region has experienced high rates of deforestation; initially for the development of coffee crops, that were replaced by pasture for livestock grazing from 1929 onwards (Monbeig, 1998). More recently, pasture has been replaced by sugarcane crops and only 4% of the original vegetation coverage remains (Nalon et al., 2008), in small and isolated fragments (Silva et al., 2007).

The three datasets include samples taken from 72 streams in MA, 29 in TA, and 91 in UPA (Fig. 1). Sampling was conducted in streams with the greatest differences in forest cover as possible. This gradient was more evident in streams in MA, which exhibited a broader range of environmental conditions compared to the narrower conditions in the other two ecoregions; the landscape in TA is still little impacted by anthropogenic activities (Borges et al., 2015), while the landscape in UPA is severely modified by human activities (Casatti et al., 2015a). Streams were not under urban influence and there is no evidence of anthropogenic activities associated with water pollution.

2.2. Fish sampling and environmental variables

Sample reaches varied from 1st to 3rd order (Sthraler, 1957) and fish were collected using electrofishing (in TA and UPA) and seine and dip nets (in MA) (see detailed methods in Bordignon et al., 2015; Casatti et al., 2015a,b). All stream reaches were sampled once in the dry season and their length was similar across regions (75-m in UPA; 80-m in TA and MA).

The environmental variables dataset included indicators of land use, habitat degradation and hydrological variables. Despite a few differences in the field protocols among regions, the overall characterization of stream reaches was comparable and included the

instream habitat, the riparian ecotone, and the catchment land cover. All stream reaches were characterized in relation to native vegetation cover in the catchment, proportion of trees and shrubs in the riparian zone, proportion of sand in the stream bottom, depth, width, and water current velocity.

We recorded the most appropriate variables for the measurement of the environmental degradation in the context of each ecoregion, thus not all variables were recorded in every ecoregion. In MA, we estimated the proportion of coarse litter in the stream bottom, since litter and fallen leaves have been shown to provide a reliable environmental indicator of habitat quality in Amazonian streams (Bordignon et al., 2015; Kemenes and Forsberg, 2014). We also calculated the proportion of macrophytes in UPA because macrophytes (mostly derived from the surrounding pasture) represent a common cover in highly deforested lowland streams (Teresa and Casatti, 2012). The proportion of native vegetation cover in a 500-m buffer around each site's catchment was used as a complementary indicator of the integrity of the surrounding vegetation in TA, given the apparent low variability of native vegetation cover in the whole catchment. These variables are good surrogates for the watershed's conservation status and local physical habitat integrity (Casatti et al., 2006; Poole and Downing, 2004).

Variables describing instream habitat conditions and riparian ecotones were measured in transversal equidistant transects along each sampled reach. The proportion of consolidated substrate, coarse litter, and aquatic macrophytes were visually estimated. Depth and wet width were measured using a meter ruler and measuring tape, respectively. Water current velocity was measured with a mechanical flow meter. Land use variables were obtained by using RapidEye imagery with a resolution of 5 m (TA) and Landsat 5 TM with a resolution of 30 m (MA and UPA), made available by the Ministério do Meio Ambiente and Instituto Nacional de Pesquisas Espaciais (INPE), respectively. The catchment limits and the drainage network were generated using satellite images

Table 1
Potential indicators assembled in groups of indices: functional diversity based on presence/absence ($FD_{p/a}$); functional diversity weighted by abundance (FD_{abund}); functional composition (mT); and taxonomic diversity (TDiv). R functions and the packages used are also shown.

Group	Potential indicators	Description	Function (package)
Functional Diversity ($FD_{p/a}$)	MPD ^a	Mean pairwise functional distance of species in the community, using the raw Euclidian distance among species.	mpd (picante)
	MNTD ^a	Mean functionally nearest species distance, using the raw Euclidian distance among species.	mntd (picante)
	FD ^b	Total branch length of a functional dendrogram (Petchey and Gaston, 2002).	pd (picante)
	FRic ^c	Volume of the convex hull generated by species position in the multidimensional functional trait space (Villéger et al., 2008).	dbFD (FD)
Functional Diversity (FD_{abund})	FGR ^d	Richness of functional groups.	dbFD (FD)
	MPD _a ^a	MPD weighted by species abundance.	mpd (picante)
	MNTD _a ^a	MNTD weighted by species abundance.	mntd (picante)
	FDiv ^c	Measures how abundance is distributed within the volume of functional trait space occupied by species, being high when more abundant species have extreme trait values (Villéger et al., 2008).	dbFD (FD)
	FDIs ^e	Mean distance of individual species in a multidimensional trait space to the centroid of all species, which in turn is dislocated towards the most abundant species (Villéger et al., 2008).	dbFD (FD)
	Rao ^f	The sum of the functional dissimilarity among all possible pairs of species, weighted by the product of the species' relative abundances (Pavoine and Dolédec 2005).	dbFD (FD)
Functional Composition (mT ^g)	mT(RD)	$mT(RD) = \sum_{i=1}^S p_i RD_i$, where S is the number of species in the community, and RD_i the value of relative depth of the i-th species in a sample.	functcomp (FD)
	mT(RCP)	$mT(RCP) = \sum_{i=1}^S p_i RCP_i$, where S is the number of species in the community and RCP_i the value of relative caudal peduncle length of the i-th species in a sample.	functcomp (FD)
	mT(CPC)	$mT(CPC) = \sum_{i=1}^S p_i CPC_i$, where S is the number of species in the community, and CPC_i the value of caudal peduncle compression index of the i-th species in a sample.	functcomp (FD)
	mT(IVF)	$mT(IVF) = \sum_{i=1}^S p_i IVF_i$, where S is the number of species in the community, and IVF_i the value of index of ventral flattening of the i-th species in a sample.	functcomp (FD)
	mT(RAP)	$mT(RAP) = \sum_{i=1}^S p_i RAP_i$, where S is the number of species in the community, and RAP_i the value of relative area of pectoral fin of the i-th species in a sample.	functcomp (FD)
	mT(EP)	$mT(EP) = \sum_{i=1}^S p_i EP_i$, where S is the number of species in the community, and EP_i the value of relative eye position of the i-th species in a sample.	functcomp (FD)
	mT(FC)	$mT(FC) = \sum_{i=1}^S p_i FC_i$, where S is the number of species in the community, and FC_i the value of fineness coefficient of the i-th species in a sample.	functcomp (FD)
Taxonomic diversity (TDiv)	Richness	Number of species per site.	specnumber (vegan)
	Simpson ^h	Equal to one minus Simpson's original measure of dominance (D). $D = \sum_{i=1}^S p_i^2$, where S is the number of species in the community, and p_i the proportion of the i-th species in a sample.	diversity (vegan)
	Shannon ⁱ	Index of Shannon (H'): $H' = H' = -\sum_{i=1}^S p_i \ln p_i$, where S is the number of species in the community, and p_i the proportion of the i-th species in a sample.	diversity (vegan)

^a Webb (2000).

^b Petchey and Gaston, (2002).

^c Villéger et al. (2008).

^d Walker, (1992).

^e Laliberté and Legendre, (2010).

^f Pavoine and Dolédec, (2005).

^g Garnier et al. (2004).

^h Simpson (1949).

ⁱ Shannon (1948).

from the Digital Elevation Model (DEM) SRTM (90 m resolution) and made freely available by the United States Geological Survey (USGS).

2.3. Functional traits

Species from the three ecoregions were characterized in relation to the same seven functional traits, thus making possible the comparison of functional diversity and composition patterns between ecoregions. All functional traits were based on morphological features which relate to habitat use, swimming capacity, and

maneuverability (Oliveira et al., 2010; Watson and Balon, 1984). Relative depth (RD), relative caudal peduncle length (RCP), caudal peduncle compression index (CPC), index of ventral flattening (IVF), relative area of pectoral fin (RAP), relative eye position (EP), and fineness coefficient (FC) were all adopted as functional traits. Habitat use and locomotion are important niche dimensions, which are associated with the response of fish to habitat structure and landscape changes (Casatti et al., 2015a,b; Pease et al., 2012; Ribeiro et al., 2016). For example, structurally less complex and degraded streams are associated with the loss of species with particular requirements, such as species with benthic and rheophilic habits,

Table 2

Mean, coefficient of variation (%), minimum, and maximum values for the environmental variables represented in the gradient of environmental degradation at the MA (n = 72), UPA (n = 91), and TA (n = 29) streams.

Variables (%)	Ecoregion	Mean	CV(%)	Minimum	Maximum
Native vegetation (catchment)	MA	40.5	82.9	0.2	100.0
Trees and shrubs	MA	65.2	58.8	0.0	100.0
Coarse litter	MA	14.4	129.2	0.0	100.0
Native vegetation (catchment)	TA	81.3	17.6	41.8	99.5
Native vegetation (500-m upstream)	TA	71.6	31.3	10.5	100.0
Trees and shrubs	UPA	24.4	134.9	0.0	100.0
Sand	UPA	90.0	19.2	15.0	100.0
Macrophytes	UPA	65.7	51.4	10.0	100.0

with a good capacity for continuous swimming, and those which inhabit turbulent waters (e.g. low values of RCP, RAP, IVF, and FC and high values of CPC, RD, and EP) (Ribeiro et al., 2016).

We obtained average morphological values of 10 individuals for each species in each ecoregion (except for those with an abundance lower than 10 individuals, for which we measured all individuals). The area measures (RAP) were estimated using Zeiss® Stereo Discovery V12 stereomicroscope and AxioVision Zeiss® image software. Species that occurred in more than one ecoregion had their individuals analyzed separately in each ecoregion in order to take into account population differences in traits. These functional data are already partially available for species sampled in the UPA ecoregion (Casatti et al., 2015a).

2.4. Taxonomic and functional indicators

We described the assemblages in each ecoregion separately in relation to four groups of indicators (Table 1): indices of functional diversity based on presence/absence ($FD_{p/a}$); indices of functional diversity weighted by abundance (FD_{abund}); indices of functional composition (mT); and indices based on taxonomic diversity (TDiv). $FD_{p/a}$ was composed of five indices: Mean Pairwise Distance of Taxa (MPD), Mean of the Nearest Distance between Taxa (MNTD), Functional Diversity (FD), Functional Richness (FRic), and Functional Group Richness (FGR) (Table 1). FD_{abund} was composed of five indices: MPD and MNTD, both weighted by species abundance, Functional Divergence (FDiv), Functional Dispersion (FDis), and the Rao's quadratic entropy. TDiv was composed of three indices: species richness, Shannon's diversity, and Simpson's diversity (Table 1).

Functional diversity indicators can be measured using different strategies (Petchey and Gaston, 2006). Some functional diversity indices (e.g., MPD, MNTD, and Rao) are computed directly based on the species pairwise functional distance (Ricotta and Szeidl, 2009). However, many others indices require more steps for their calculation, such as indices based on the distribution of species within multidimensional functional space (e.g., FRic, FDiv, and FDis), whose dimensions are the traits (Villéger et al., 2008), and indices based on dendrograms (e.g., FD and FGR), in which the species are the tips and their relative position on the tree reflect the hierarchy in the functional dissimilarities (Petchey and Gaston, 2002). These indices are the most widely used in the literature (Maire et al., 2015).

The multidimensional functional space used for the calculation of FRic, FDiv, and FDis was defined by vectors summarizing the trait dissimilarities between species obtained by a Principal Coordinates Analysis (PCoA) (Laliberté and Legendre, 2010). The dimensionality reduction was needed because some sites had less species than traits, which prevents the calculation of these indices (Villéger et al., 2008). Dendrogram-based indices (FD and FGR) were calculated using dendrograms created from the pairwise euclidean distance among species based on functional traits, using the Unweighted Pair Group Method with Arithmetic mean (UPGMA). We formed

functional groups for FGR calculations considering the threshold of 0.7 in each functional dendrogram. Values for mT were calculated for each functional trait separately and they consisted of the community-weighted mean of each trait (Table 1). We log-transformed functional diversity indicators and species richness in order to reduce the influence of extreme values and to meet the requirements of normality in the subsequent statistical analyses. R (version 3.2.2) was used to calculate all indices and to perform all statistical analyses (R Core Team, 2012).

2.5. Data analysis

Our analysis was carried out in three steps: 1) obtaining the gradient of environmental degradation based on environmental variables; 2) assessing the performance of indices by testing their response to the environmental gradient; 3) comparing the performance of indices among groups of indices and among ecoregions.

Step 1: we used a principal component analysis (PCA) from a correlation matrix that included non-collinear environmental variables (assessed by Pearson correlation) to emphasize the most important environmental gradients in each ecoregion. We used the broken-stick criterion for assessing the importance of the environmental variables to the principal components (Peres-Neto et al., 2003). Preliminary analysis of data indicated that the gradient of environmental degradation in the three ecoregions was not associated with the natural hydrological gradient. If they were, land use and habitat degradation variables and hydrological variables would be summarized by different axes, so that we could use the axis representing the formers as a composite predictor variable (i.e. gradient of environmental degradation).

Step 2: because stream fish assemblages are strongly influenced by the natural hydrological gradient (Ibañez et al., 2009), we used the residuals of the regressions between $FD_{p/a}$, FD_{abund} , mT, and TDiv with the three hydrological variables (width, depth, and water velocity; all standardized by the Z-score method) as potential indicators. Therefore, our taxonomic and functional indicators represent any variation that could not be explained by the natural hydrological gradient. We thus assessed all indices (the residuals) against the gradient of environmental degradation (site scores from the components extracted by PCA in step 1) by using linear regression. We used the resulting R-squared values as performance indicators of the ability of each index to detect the gradient of environmental degradation.

Step 3: in order to evaluate the differential performance of indices to detect the environmental gradient we compared the mean performance of the indices (R-squared) among groups of indices ($FD_{p/a}$, FD_{abund} , mT, and TDiv) and among ecoregions using two-way Analysis of Variance, followed by Fisher's Least Significant Difference (LSD) post hoc test. A significant main effect of group of indices would indicate differential performance among indices, while a significant main effect of region would indicate that the predictive power of indices varies across ecoregions. Finally, an interaction effect would indicate that the effect of indices is dif-

ferent across ecoregions, which would mean that the performance of indices is not consistent across ecoregions. The latter result is expected, since according to our hypothesis, the performance of functional trait indicators is greater than taxonomic indicators and this varies among ecoregions, according to the length of the environmental gradient.

In order to evaluate the performance and consistency in the response of indices individually, we plotted indices in relation to their average performance across ecoregions and their inter-region variation (measured by the coefficient of variation across ecoregions). The inter-region variation was used as an indicator of consistency for the capacity of indices to predict the environmental gradient.

3. Results

3.1. Environmental gradient and biological data

The first two axes of PCA explained 55.97%, 53.87%, and 50.3% of the total variation in the environmental data of MA, TA, and UPA, respectively (see Supplementary material for detailed information). The first axis for MA and UPA and the second axis for TA summarized variables describing land use and habitat degradation and were retained for subsequent analysis. These axes accounted for 38.1%, 29.7%, and 20.24% of the total variation in data, respectively. The variables significantly associated with the retained axes were: proportion of native vegetation cover in the catchment, proportion of trees and shrubs in the riparian zone and proportion of coarse litter in the stream bottom in MA; proportion of native vegetation cover in the catchment and proportion of native vegetation cover in a 500-m buffer around the site's catchment in TA; proportion of tree and shrubs in the riparian zone, proportion of macrophytes in the instream habitat, and the proportion of sand in the stream bottom (Table 2).

We recorded 131 species in MA, 59 in UPA, and 47 in TA (complete list in the Table S1 of the supplementary material). Richness varied from 7 to 36 (mean = 20.1) in MA, 7–28 (mean = 17) in TA, and 3–21 (mean = 10.21) in UPA. Non-native species occurred in UPA (three species) and MA (one species), but not in TA. Given that the data analysis with and without non-native species in the dataset showed similar results we decided not to include non-native species in our analysis in order to make the patterns comparable.

Communities from the three ecoregions were characterized in relation to the 20 indicators. For the calculation of indices based on the multidimensional functional space (FRic, FDis, and FDiv), there was the necessity for the reduction of the dimensionality of the functional trait matrices because the number of traits were higher than the number of species in some communities (see Material & Methods). Six axes for MA and TA and two for UPA were retained, summarizing 95.2, 97.8, and 61.1% of the total interspecific trait variability, respectively. Furthermore, the cophenetic coefficient calculated with the functional dendrogram, used for FD and FGR calculations, was 0.87, 0.83, and 0.81 for MA, TA, and UPA, respectively; indicating a good representation of the original similarities among species.

3.2. Performance of the group of indicators

We found a significant interaction effect ($F_{(8,48)} = 3.75$, $P = 0.004$) between groups of indices and ecoregions in the performance of indices in detecting the gradient of environmental degradation (Fig. 2). For MA, all groups of functional indicators performed better than the taxonomic diversity group (LSD post hoc test, $p < 0.01$, Fig. 2), and functional diversity indicators (FD_{pa} and FD_{abund}) per-

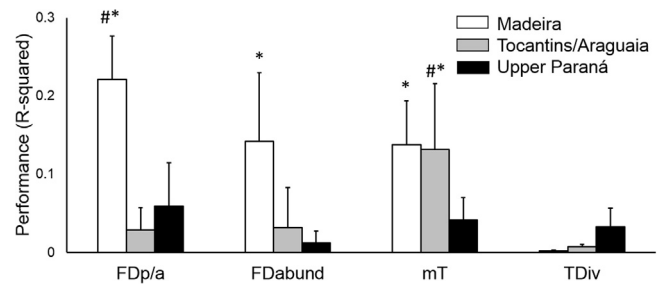


Fig. 2. Mean \pm sd of the R-squared, indicating the performance of the functional diversity indices based on presence and absence (FD_{pa}), functional diversity indices weighted by abundance (FD_{abund}), indices based on the mean of traits (mT), and taxonomic diversity indices (TDiv) in the Madeira, Tocantins-Araguaia and Upper Paraná ecoregions. * indicate statistically higher performance than the other ecoregions without the asterisks for a given group of indicator at $p < 0.05$ (LSD post hoc test); # indicate statistically higher performance of the group of indicator in relation to the all others groups for a given ecoregion at $p < 0.05$ (LSD post hoc test).

Table 3

Performance (R-squared) of functional and taxonomic indicators in the Madeira (MA), Tocantins-Araguaia (TA) and Upper Paraná (UPA) ecoregions. FD_{pa} : functional diversity indices based on presence and absence; FD_{abund} : functional diversity indices weighted by abundance; mT: indices based on the mean of traits; TDiv: taxonomic diversity indices. For indices' codes see Table 1.

Group of indicators	Indicators	MA	TA	UPA
FD_{pa}	MPD	0.22	0.01	0.00
	MNTD	0.40	0.08	0.00
	FD	0.10	0.01	0.07
	FRic	0.10	0.03	0.11
	FGR	0.29	0.01	0.11
FD_{abund}	MPD_a	0.14	0.00	0.01
	$MNTD_a$	0.26	0.12	0.00
	FDis	0.15	0.01	0.01
	FDiv	0.01	0.02	0.04
	Rao	0.15	0.01	0.01
mT	RD	0.22	0.13	0.00
	RCP	0.15	0.22	0.07
	CPC	0.12	0.23	0.05
	IAV	0.06	0.05	0.06
	RAP	0.19	0.19	0.02
TDiv	PRO	0.12	0.11	0.02
	FC	0.09	0.00	0.07
	Richness	0.00	0.00	0.06
	Shannon	0.00	0.01	0.02
	Simpson	0.00	0.01	0.01

formed better than the corresponding indicators in TA and UPA (LSD post hoc test, $p < 0.01$, Fig. 2). In TA, functional composition indicators (mT) were the highest performing indices (LSD post hoc test, $p < 0.01$, Fig. 2) and worked equally well as mT indices in MA. In UPA, functional and taxonomic indicators had low predictive power, with no variation among them (LSD post hoc test, $p > 0.49$, Fig. 2).

3.3. Performance of the individual indicators

The individual performance of indicators varied among indices and ecoregions (Table 3). The indicators with better performance in MA were MNTD ($R^2 = 0.40$), FGR ($R^2 = 0.29$), MPD ($R^2 = 0.22$), and mT(RD) ($R^2 = 0.22$). In TA three mT (CPC, RCP, and RAP) had the best performance ($R^2 = 0.23$; 0.22; 0.19, respectively). In UPA the best performing indicators were of FRic and FGR ($R^2 = 0.11$). Taxonomic diversity indicators had the worst performance in all three ecoregions ($R^2 < 0.06$) (Table 3).

At least three of the seven functional traits (mT) had the highest average performance and consistency (lower inter-region variation) (Fig. 3). Functional diversity indicators (FD_{pa} and FD_{abund}) had variable average performance and low consistency, while tax-

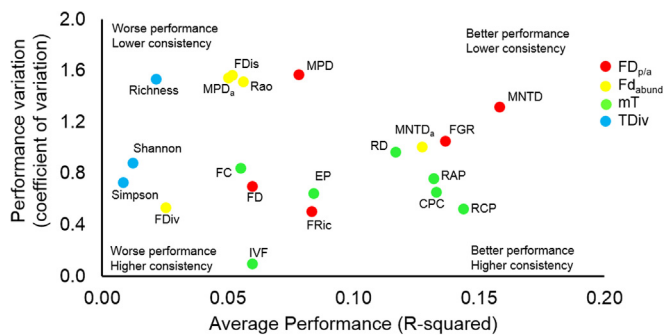


Fig. 3. Average performance of functional and taxonomic indicators across ecoregions and the inter-region variation in the performance. $FD_{p/a}$: functional diversity indices based on presence and absence; FD_{abund} : functional diversity indices weighted by abundance; mT: indices based on the mean of traits; TDIV: taxonomic diversity indices. For indices' codes see Table 1.

onomic diversity indicators, had the worst average performance (Fig. 3).

4. Discussion

We tested whether indicators of fish communities are associated with gradients of environmental degradation in streams. We expected that trait-based indicators (FD and mT) would perform better because the spatial distribution of species along the gradients of human impacts is known to be associated with their traits (Flynn et al., 2009). Our results support the notion that the general condition of streams regarding their land use and habitat quality are captured by fish communities in streams from the three Neotropical ecoregions studied here, but not in the same way. While the functional structure of Amazonian communities (MA) exhibits a stronger environmental signature, communities from the most severely degraded ecoregion (UPA) showed a more unpredictable structure. Furthermore, the capacity of fish community indicators to predict the environmental gradient is variable within- and among-groups of indicators and among ecoregions, suggesting a context-dependent performance.

4.1. Environmental gradient

The gradient we studied encompasses heavily degraded streams, with large amounts of grass on stream banks and sandy stream bottoms, to better conserved streams, with higher amounts of coarse litter in stream channels, and native vegetation in the landscape (Bordignon et al., 2015; Casatti et al., 2015a; Leal et al., 2016). For two of the three ecoregions we studied (MA and UPA) variables associated with anthropogenic influences are the main source of environmental variability, as shown in the PCA results. In UPA, variables describing the instream habitat and the riparian ecotone were most important while in MA native vegetation in the catchment also contribute to environmental variability. In contrast, the natural hydrological gradient in TA is more evident, with the gradient of deforestation in the catchment acting as a secondary sources of variation among streams. These patterns reinforce the differences in the intensities and histories of land use and habitat degradation. In TA, the landscape is relatively well conserved, which makes the natural differences among streams more evident. Contrary, to UPA narrow riparian forest strips with variable width and conservation status are usually the only native remnants in the entire catchment, which explains the low variation in the catchment variables and higher importance of local variables for among-stream variability.

The proportion of sand in stream bottoms was associated with the anthropogenic gradient in UPA, while in MA the proportion

of sand in stream bottoms was associated with the gradient of hydrological variation. In streams from UPA, the greater deposition of fine substrate (sand) when compared to the consolidated substrate (e.g., cobbles, boulders, rocks) is an indicator of siltation and has been associated with low habitat quality for fishes (Casatti et al., 2006). However, sand and fine sediments are naturally present in the streambed of Amazonian streams (Leal et al., 2016), offering a potential explanation for the mismatch between the variation in substrate composition and the variables associated with anthropogenic influences. Furthermore, previous studies have also showed that substrate composition influences the structure of fish communities in UPA more strongly (Casatti et al., 2006; Ribeiro et al., 2016) than in MA (Bordignon et al., 2015). Therefore, these results reinforce that the variables composing the environmental gradient in each ecoregion are reliable indicators of the loss of physical integrity of instream habitats and degradation of native vegetation in the ecotone, typical alterations in agroecosystems (Carvalho and Tejerina-Garro, 2015a; Casatti et al., 2006; Leal et al., 2016).

4.2. Performance of the groups of indicators

Our results show that taxonomic indicators are consistently less predictive of the environmental gradient than trait-based indicators, corroborating our hypothesis. These results reveal that the loss of gain of species and the changes in species abundance *per se* are not predictable along the environmental gradient. However, when these changes are evaluated in a trait-based perspective the predictive power of the indicators increases. This mismatch between taxonomic and functional diversity indicators is well-documented in the literature (Carvalho and Tejerina-Garro, 2015b; Devictor et al., 2010; Gonçalves-Souza et al., 2015). Indeed, changes in species richness may not be directly related to changes in functional diversity, revealing different processes that structure assemblages, such as environmental filtering and niche complementarity (Mayfield et al., 2010).

The higher predictive power of functional trait indicators in MA is in accordance with our expectations. More specialized species and functionally overdispersed assemblages are found in near pristine streams from this ecoregion, in contrast to communities with a dominance of generalist and redundant species, a common scenario in deforested streams (Bordignon et al., 2015). Functional diversity (FD), as well as functional composition indicators (mT), successfully captured these changes. In TA, only mT indicators had higher performance, suggesting that the functional turnover (*sensu* Villéger et al., 2013) was the dominant process structuring stream fish assemblages. Perhaps, the narrower environmental gradient, in the absence of heavily degraded streams, prevented changes in functional diversity, while the changes in species abundance and the replacement of species with contrasting traits resulted in changes in functional composition.

In contrast to the MA and TA ecoregions discussed above, fish species from UPA were unpredictably distributed across the environmental gradient, as suggested by the lower performance of all groups of indicators. This region has a relatively older history of human influences, with the highest rates of deforestation, which started earlier than in the other two ecoregions. Native forest remnants comprise only 4% of the original vegetation coverage (Nalon et al., 2008) and the higher level of physical habitat degradation experienced by aquatic communities has previously been documented in this ecoregion (Casatti et al., 2009, 2015a). Considering that species tend to converge in terms of their traits in response to strong environmental constraints (Keddy, 1992), we would expect a high level of functional redundancy in the regional species pool. Functionally redundant communities (i.e., communities highly dominated by a few traits) present higher functional

stability (Pillar et al., 2013), which means that the spatial variation in the species composition is not accompanied by changes in the functional structure in such communities, limiting our capacity to discriminate environmental gradients with these communities (low performance of indicators). Indeed, with the exception of a few streams located near some isolated forest fragments, fish assemblages from UPA show high redundancy, probably as a legacy of the historical filtering process (Casatti et al., 2015a).

We also hypothesized that narrower gradients would be predicted mainly by indices weighted by abundance. These expectations are based on the idea that such indices would be more sensitive to lower levels of perturbation, because changes in relative abundance are early signals of environmental change (Mouillot et al., 2013a). Thus, we would expect better performance from FD_{abund} in the UPA and TA ecoregions. Our data do not corroborate this hypothesis, as FD_{abund} had similar, or worse performance, than $FD_{p/a}$ indices. This is conceivably due to the fact that less abundant species are more important in determining the performance of the indices, which is the case whether rare species have a more predictable spatial distribution along the environmental gradient, or not (Petsch et al., 2015). When indices are weighted by abundance, these influences are overcome by dominant species. Furthermore, rare species tend to support unique combinations of traits, contributing disproportionately to the functional diversity of communities (Leitão et al., 2016; Mouillot et al., 2013b), making $FD_{p/a}$ as, or even more, informative than abundance weighted indices.

4.3. Performance of individual indicators

Higher average performance and lower inter-region variation are good characteristics for reliable bioindicators across ecoregions. In our study, functional composition (mT) had such characteristics. The higher predictive power of mT is consistent with the findings from temperate streams and rivers (Carlisle and Hawkins, 2008; Statzner et al., 2005), and estuarine ecosystems (van der Linden et al., 2016). In our case, mT indices represent the relative importance of morphological traits related to habitat use and locomotion at the community level. Their higher predictive power indicates a spatial turnover of species with different niche requirements across the environmental gradient. For example, water column swimmers and limnophilic species tend to be replaced by benthic and rheophilic species in response to changes in instream conditions associated with the deforestation of areas surrounding streams (Casatti et al., 2012, 2015a). Additionally, mT indicators would have the additional advantage of being easier to estimate in comparison to FD indicators (Vandewalle et al., 2010). Thus, in regions where autoecological knowledge is lacking for the majority of species, as is the case in the tropics, the use of functional composition indicators based on habitat use and locomotion seem to be a good choice for assessing the environmental quality in running waters.

The best performing functional diversity indices are MNTD and FGR. However, they are less consistent, having the best performance in MA but not in the other two ecoregions. MNTD is an index sensitive to changes in the terminal branches of a functional dendrogram (Webb, 2000), while FGR is sensitive to the addition or loss of groups of species that share traits (i.e. functional groups). Thus, these indices should capture different processes in the response of stream assemblages across the environmental gradient. While MNTD should capture small changes in the functional space occupied by species, i.e., the loss of redundant species, FGR responds to major drift in the functional structure of communities. In fact, these are complementary responses that could occur in communities along a large breadth of environmental conditions, as found in MA.

4.4. Implications for environmental monitoring

The main implication of our study for applied ecology is recognizing that functional indicators outperform taxonomic indicators at detecting gradients of environmental degradation. The former have the additional advantage of greater potential for transferability across regions (Vandewalle et al., 2010). The traits we used provide ecologically meaningful information regarding locomotion and habitat use of species (Oliveira et al., 2010), and could be easily measured by trained technicians. However, our results do not support the existence of a universal indicator (Hevia et al., 2016), as the performance of indicators depends on the ecoregion and probably the breadth of the environmental gradient.

Our results of the average of the individual performance of the indices show that the better indicators (higher performance and consistency) had only approximately 15% of their variation explained by the environmental gradient on average (see Fig. 3). However, the average values are influenced by the variability in the response of indicators, especially the low diversity–environment relationship in UPA. Considering the other two ecoregions, a higher variation in the functional indicators are explained by the environmental gradient (~20 to 40%), which is relatively high when compared with other studies (Casatti et al., 2015a; Moretti et al., 2009; Vandewalle et al., 2010), reinforcing the predictive power of the functional indicators.

4.5. Concluding remarks

The Neotropical region has one of the richest biotas in the world, supporting high functional diversity (Toussaint et al., 2016) and essential ecosystem services (Tundisi and Matsumura-Tundisi, 2008), but the development of management and conservation tools for protect this diversity have been incipient (Ruaro and Gubiani, 2013). In this context, our study provides one the first attempts to comparatively evaluate the performance of different functional trait indicators in detecting environmental degradation in different ecoregions. This approach can be insightful to the understanding of the consistency in the performance of ecological indicators, which is especially relevant in the Neotropical region, where comparative studies on stream fish on broader spatial scale are scarce (Dias et al., 2016).

In summary, our results indicate that functional trait indicators are better than traditional descriptors of communities at predicting fish responses to a gradient of environmental degradation. We also highlight the need for caution when generalizing functional diversity indicators across ecoregions, as the performance of the majority are context-dependent, although functional composition indicators are promising transferable indicators of environmental quality.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2016.12.041>.

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